

***Alpheus angulatus*, a new species of snapping shrimp from the
Gulf of Mexico and northwestern Atlantic, with a
redescription of *A. heterochaelis* Say, 1818
(Decapoda: Caridea: Alpheidae)**

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Abstract.—Two species of the Edwardsii-group of snapping shrimp, *Alpheus heterochaelis* Say and *A. estuariensis* Christoffersen, have been recorded from coastal estuarine habitats of the Gulf of Mexico and Atlantic coasts of the United States. A new species, *A. angulatus*, has been discovered to inhabit these habitats across this range and is described and illustrated. The new species is morphologically similar to *A. armillatus*, the latter being a tropical species. A redescription with illustrations of *A. heterochaelis* is also provided herein.

The Edwardsii species group of *Alpheus* consists of at least 10 western Atlantic species (Chace 1972; Christoffersen 1979, 1984; Williams 1984; Abele & Kim 1986), of which *Alpheus heterochaelis* Say, 1818, is the most abundant and widely distributed. *Alpheus heterochaelis* was originally described from Amelia Island, Nassau County, Florida, and has been reported to range from the lower Chesapeake Bay to Aransas County, Texas, Cuba, Curaçao, Surinam, and possibly to São Paulo, Brazil (Chace 1972, Williams 1984).

A variety of studies have been done concerning the biology of *A. heterochaelis* (for example, Wilson 1903, Nolan & Salmon 1970, Knowlton 1973, Conover & Miller 1978, Mellon & Stephens 1978). Despite the abundance of studies on *A. heterochaelis*, the geographic limits and the systematic status of this species remain problematic. Based on apparent misidentifications of West Indian and Brazilian specimens, Chace (1972) questioned the occurrence of *A. heterochaelis* south of Surinam. Knowlton (1973) noted differences in egg size between laboratory reared *A. heterochaelis* from North

Carolina and south Florida, and proposed that *A. heterochaelis* comprised two or more species. From a reevaluation of *Alpheus* inhabiting shallow-estuarine environments of the western Atlantic, Christoffersen (1984) suggested the existence of a species complex, and described a new species, *A. estuariensis* (holotype from the Rio Potengi estuary, Rio Grande do Norte, Brazil), ranging from the east coast of Florida into the Gulf of Mexico from Mississippi to Texas; Cuba; Dominican Republic; Trinidad; Curaçao; and from Ceará to Paraná, Brazil. Christoffersen (1984) further concluded that the *Alpheus* occurring in the northern Gulf of Mexico represents *A. estuariensis*, and described the range of *A. heterochaelis* to be from North Carolina to Paraíba, Brazil. However, using Christoffersen's (1984) key, specimens from Galveston were identified by the author as *A. heterochaelis*. Thus, plus a reexamination of museum specimens of *A. estuariensis* from the northern Gulf of Mexico suggest the existence of taxonomic ambiguity concerning the Edwardsii group of *Alpheus* from the coastal waters of the Gulf of Mexico and northwestern Atlantic.

An assessment of allozymic variation of specimens of *Alpheus* from Texas revealed the existence of two discrete and markedly different gene pools (McClure & Greenbaum 1994). Additional allozymic data (unpublished) indicate that these forms are sympatric throughout the northern Gulf of Mexico and Northwestern Atlantic coasts as far north as Beaufort, North Carolina. The present study was designed to provide morphological descriptions and identifications of the two electrophoretically identified species.

Materials and Methods

Snapping shrimps were collected at low tide by dip net in intertidal and shallow subtidal habitats consisting of sand or mud bottoms covered with oyster clumps or rocks. Shrimps were collected in coastal waters from south Texas to North Carolina (see Appendix for localities). Shrimps were stored at -80°C to fully preserve color patterns. Starch-gel electrophoresis (McClure & Greenbaum 1994) was used to sort the individuals into discrete electromorphic classes. Morphological characters were then assessed and compared with museum material and descriptions in the literature. Total Length (TL) of specimens is the combined measurements of the carapace, abdominal, and telson lengths.

Museum specimens of *A. heterochaelis*, *A. estuariensis*, *A. nuttingi*, and *A. armillatus* were obtained from the following institutions: Marine Research Division, Florida Department of Natural Resources, St. Petersburg, Florida (FBSC); Marine Environmental Sciences Consortium, Tuscaloosa, Alabama (MESOC); Texas A&I University, Kingsville, Texas (TAI); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); Muséum national D'Histoire naturelle, Paris, France (MNHN); Lamar University collection, Beaumont, Texas (LU). The original type material of *A. heterochaelis* and *A.*

armillatus is not available; it is likely that the specimens have been lost. As the only detailed descriptions of *A. heterochaelis* are from the Carolinas (Christoffersen 1984), comparisons to this species were from material from the type locality and from the Carolinas. For *A. armillatus*, specimens from the type locality (Antilles) were used as a reference. Type material of the two species described here have been deposited in the USNM.

Alpheus angulatus, new species Figs. 1, 2

Crangon armillatus.—Hay & Shore, 1918: 386, fig. 9. (not *Alpheus armillatus* Milne-Edwards, 1837).

Alpheus estuariensis.—Christoffersen, 1984: 191 (in part, see discussion).

Alpheus armillatus.—Chace, 1972:62 (in part, see discussion).

Holotype.—Male, 28 mm TL, on mud under rocks and rubble, South Padre Island, Texas, Laguna Madre just north of Brazos-Santiago Pass, coll. M. K. Wicksten, 4 Jul 1992, USNM 266804.

Material examined.—See Appendix.

Diagnosis.—Rostro-orbital depressions abrupt posteriorly. Ventral margin of carapace pronounced at an angle ventrally posterior to second pereopods. Minor claw of male not balaeniceps-shaped. Spine present on merus of first pereopod. Third and fourth pereopods with movable spine on ischium, lacking on fifth pereopod.

Description of holotype.—Rostrum reaching 0.5 length of first antennular segment; in form of raised crest extending beyond base of eyestalks and widening into flat triangular area (Fig. 1A). Ocular hoods prominent and unarmed, separated from rostrum by adrostral depressions abrupt posteriorly (Fig. 1A). Ocular hood width 0.27 times length of carapace. Carapace as figured (Fig. 1C), 0.35 times TL (range 0.31–0.40 for all specimens examined). Carapace smooth, posterior of carapace with cardiac notch;

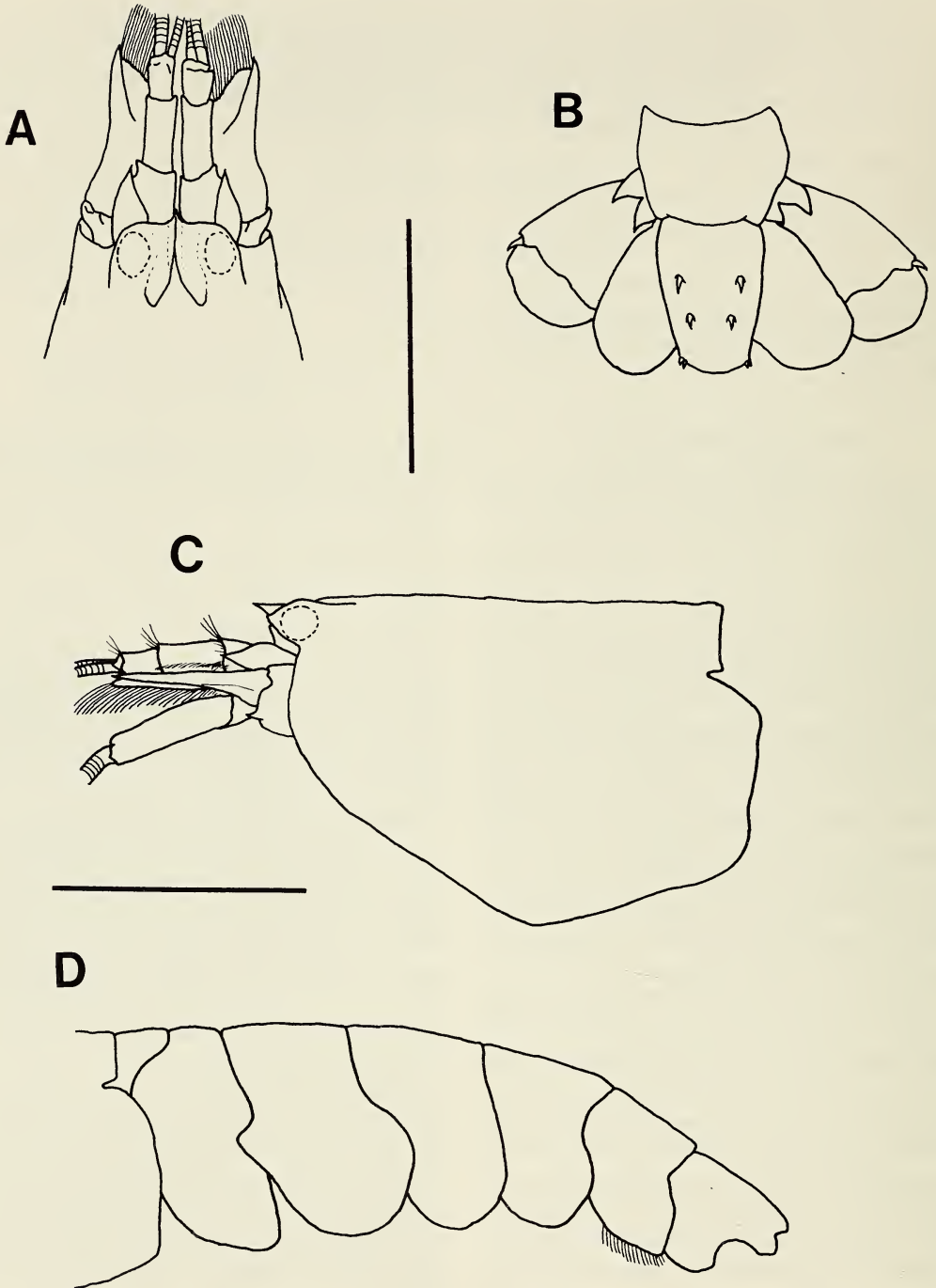


Fig. 1. *Alpheus angulatus*, new species. Adult male (holotype) from South Padre Island, Texas (TL = 28 mm). A, anterior carapace and antennae, dorsal; B, sixth abdominal somite, telson and uropods, dorsal; C, carapace and antennae, lateral; D, abdominal pleura, lateral. Bar indicates 5 mm.

ventral margin acute ventrally just posterior to articulation of second pereopod.

Abdomen as figured (Fig. 1D), 0.55 times total length (range 0.44–0.56). Pleura of abdominal somites 1 through 5 with ventral margins rounded. Sixth abdominal pleura with ventral margin acute posteroventrally. Telson (Fig. 1B) 0.11 times total length (range 0.09–0.14). Proximal telson width 0.67 of length, distal width about 0.5 of length; 2 pairs of dorsal spines, anterior-most pair positioned about 0.4 of telson length, posteriormost pair positioned at 0.67; posterior margin convex, with 2 pairs of lateral spines, space between spines with double row of setae.

Antennular peduncle with stylocerite dorsally flattened, terminating anteriorly at sharp point which reaches anterior margin of first antennular segment; second antennular segment longer than first and about 1.5 times as long as third (Fig. 1A, C).

Antennal spine reaching end of antennal peduncle, and just overreaching antennal scale; concave at middle and faintly convex at distal tip. Basal segment of antennal peduncle armed with spine ventrolaterally (Fig. 1A, C).

Mandible with 10 teeth. Third maxilliped reaching just beyond end of antennal peduncle; terminal article setose.

First pereopods (Fig. 2A, B, C) strongly chelate and unequal; merus armed with spine distoventrally. Major chela thick, setose distally; propodus length 0.51 times total body length (range 0.28–0.56); upper and lower margins deeply notched proximal to articulation of dactyl, upper notch width about 0.04 of propodus length, lower notch width about 0.11 of propodus length; maximum propodus height about 0.46 times length; dactyl length about 0.36 times propodus length; hand height with dactyl closed about 0.35 times propodus length; dactyl with entire upper and distal margins rounded, with setae arranged in tufts; opposable margin of dactyl with molar process tilted at angle to axis of dactyl; sculpture of prop-

odus as figured (Fig. 2A, B), with upper and lower notches forming saddle-like depressions (extending about 0.07 and 0.11 times length of propodus, respectively) into the lateral surfaces of propodus; upper notch positioned about 0.5 the length of propodus, lower notch positioned about 0.61, having tuft of setae on proximal end of lower notch; angular area of upper mesial surface of fixed finger rounded, having granular texture and tufts of setae; distal end of propodus rounded, with tufts of setae. Minor chela robust and setose, with setal tufts increasing distally on both propodus and dactyl (Fig. 2C); not sexually dimorphic, lacking balaeniceps setose crest on dactyl; propodus 0.33 times total body length (range 0.15–0.37 for specimens examined); propodus height about 0.30 times length in both sexes; dactyl length about 0.5 times that of propodus length in both sexes.

Second pereopods slender and weakly chelate (Fig. 2D); carpus subdivided into 5 articles decreasing in length as follows (numbered from the proximal end); 1, 2, 5, 3 = 4. Third and fourth pereopods with ventral movable spine on ischium (Fig. 2E, F); dactyli simple; third pereopod propodus with 7 stout spines and 3 or 4 smaller alternating lateral spines, fourth with 8 stout spines and 5 or 6 alternating lateral spines. Fifth pereopod (Fig. 2G) with 8 or 9 spines on the propodus and several lateral bands of comb-like setae extending on distal half; ischium without spine. Second pleopod of male with appendix masculina shorter than appendix interna (Fig. 2H).

Coloration.—Overall dark olive green to brown, occasionally with blue tones around orbits, distal half of abdomen, and telson; body speckled with tiny brown or red-brown spots. Major chela dark olive green throughout mesial surface, unspeckled; upper and lower notches either colored as rest or major chela or lightened to pale yellow, rarely with blue; inner surface of major chela white or pale yellow, occasionally bluish; fingertips pale yellow or white. Minor chela dark olive

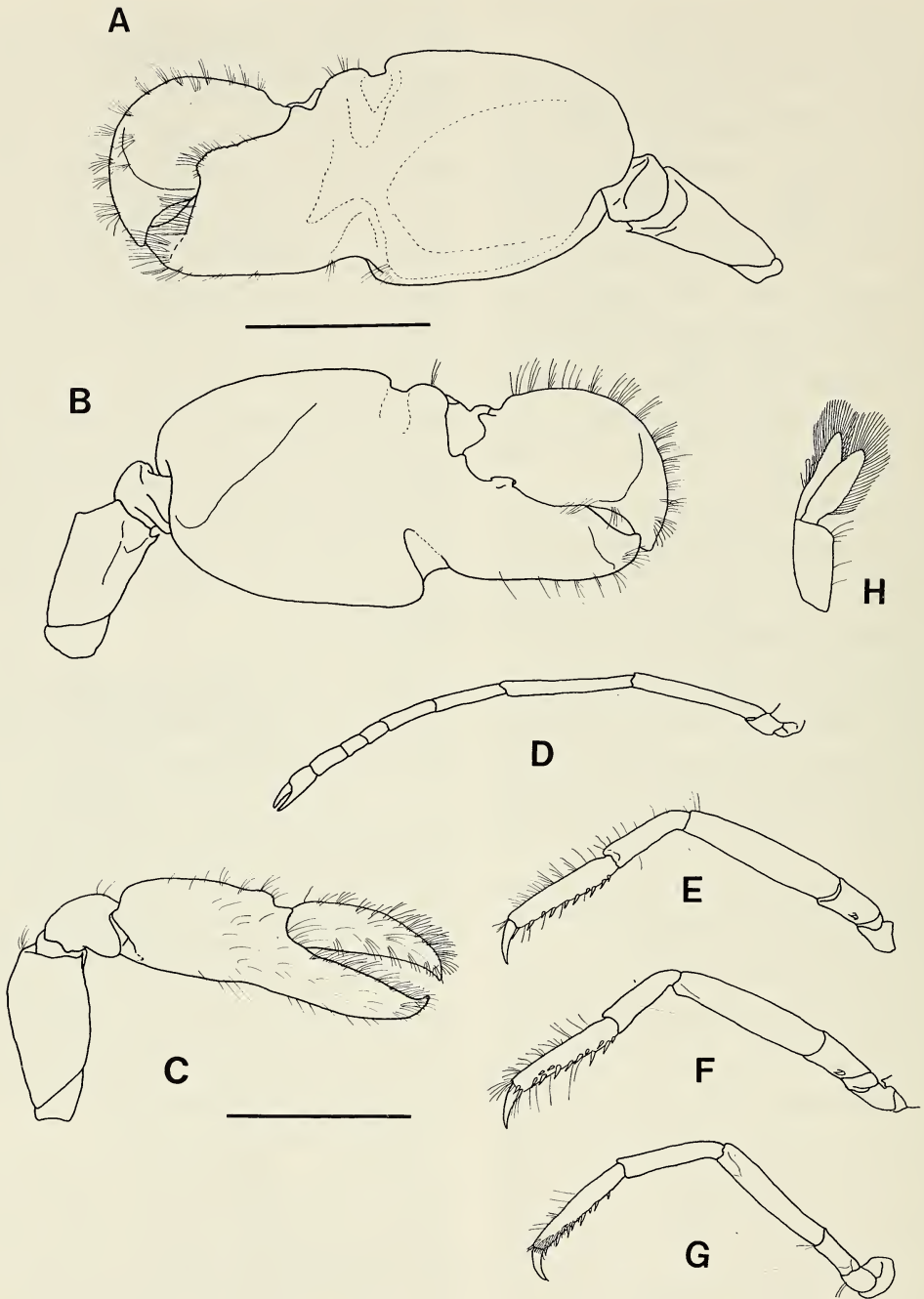


Fig. 2. *Alpheus angulatus*, new species. A, major first pereopod (right), dorsal; B, same, ventral; C, minor first pereopod (left); D, left second pereopod; E, left third pereopod; F, left fourth pereopod; G, left fifth pereopod; H, left second pleopod. Bar indicates 5 mm.

green. Second to fifth pereopods translucent to reddish, lightly speckled with reddish brown spots or mottled with red. Telson colored as abdomen, highly speckled with tiny brown or red-brown spots; uropods often bluish throughout, occasionally blue distally.

Size.—Total length for males ranging 17 to 38 mm, females 17 to 35 mm.

Etymology.—Specific name derived from the shape of the ventral margin of the carapace, which contains a pronounced angle posterior to the second pereopods.

Range.—The known range for this species is throughout the northern Gulf of Mexico and northwestern Atlantic as far north as Beaufort, North Carolina, and as far south as Quintana Roo, Mexico, and Haiti.

Habitat.—Intertidal and shallow waters in bays and other quiet waters consisting of mud bottoms with oyster clumps or rocks and rubble.

Alpheus heterochaelis Say, 1818

Figs. 3, 4

Alpheus heterochaelis Say, 1818:243.—Milne-Edwards, 1837:356.—Kingsley, 1878a:194, 1878b:329, 1879:417.—Brooks & Herrick, 1892:376, pl. 2.—Coutière, 1910:485.—Verrill, 1922:76, pl. 22, figs. 1, 2, 4a–c; pl. 24 figs. 7, 7a; pl. 30, figs. 1-1a, 1t, 2a–2e; pl. 33, figs. 1, 2.—Holthuis, 1959:102.—Williams, 1965:66, fig. 54, 1984:95, fig. 65.—Chace, 1972:67.—Coelho & Ramos, 1972:148.—Christoffersen, 1984:200, figs. 5–7.

Crangon heterochaelis.—Hay & Shore, 1918:386, fig. 8.—Schmitt 1935:144.

Holotype.—Not extant, Amelia Island, Nassau County, Florida.

Neotype.—1 male, 31 mm total length, Fort Saint George Inlet (8 miles south of Amelia Island), Duval County, Florida, intertidal habitat consisting of hard mud and clumps of oysters, coll. M. R. McClure and L. S. McClure, 25 May 1992, USNM 268646.

Material examined.—See Appendix.

Diagnosis.—Rostro-orbital depressions not abrupt posteriorly. Ventral margin of carapace evenly rounded, not pronounced at an angle ventrally posterior to second pereopods. Minor claw of male balaeniceps-shaped. Spine absent on merus of first pereopod. Third, fourth, and fifth pereopods with movable spine on ischium.

Description of neotype.—Rostrum carinate, reaching 0.5 length of first antennular segment, extending about as far as base of eyestalks. Ocular hoods prominent and unarmed, separated from rostrum by shallow adrostral depression. Ocular hood width 0.25 times length of carapace (Fig. 3A, C). Carapace as figured (Fig. 3C), 0.35 times TL (range 0.32–0.40 for all specimens examined). Carapace smooth, posterior with cardiac notch.

Abdomen as figured (Fig. 3D), 0.52 times total length (range 0.45–0.55). Pleura of abdominal somites 1 through 5 with ventral margins rounded. Sixth abdominal pleura with ventral margin acutely rounded posteroventrally. Telson (Fig. 3B) 0.12 times total length (range 0.09–0.14). Proximal telson width about 0.67 of length, distal width about 0.5 of length; 2 pairs of dorsal spines, anteriormost pair positioned about 0.5 of telson length, posteriormost pair positioned almost 0.75; posterior margin convex, with 2 pairs of lateral spines, space between spines with double row of setae (Fig. 3B).

Antennular peduncle with stylocerite dorsally flattened and terminating anteriorly at a sharp point which reaches anterior margin of first antennular segment; second antennular segment longer than first and about 1.4 times as long as third (Fig. 3A, C).

Antennal spine reaching end of antennal peduncle, and just overreaching antennal scale; spine faintly convex at distal tip, straight or slightly concave at middle. Basal segment of antennal peduncle armed ventrolaterally (Fig. 3A, C).

Mandible with 9 teeth. Third maxilliped

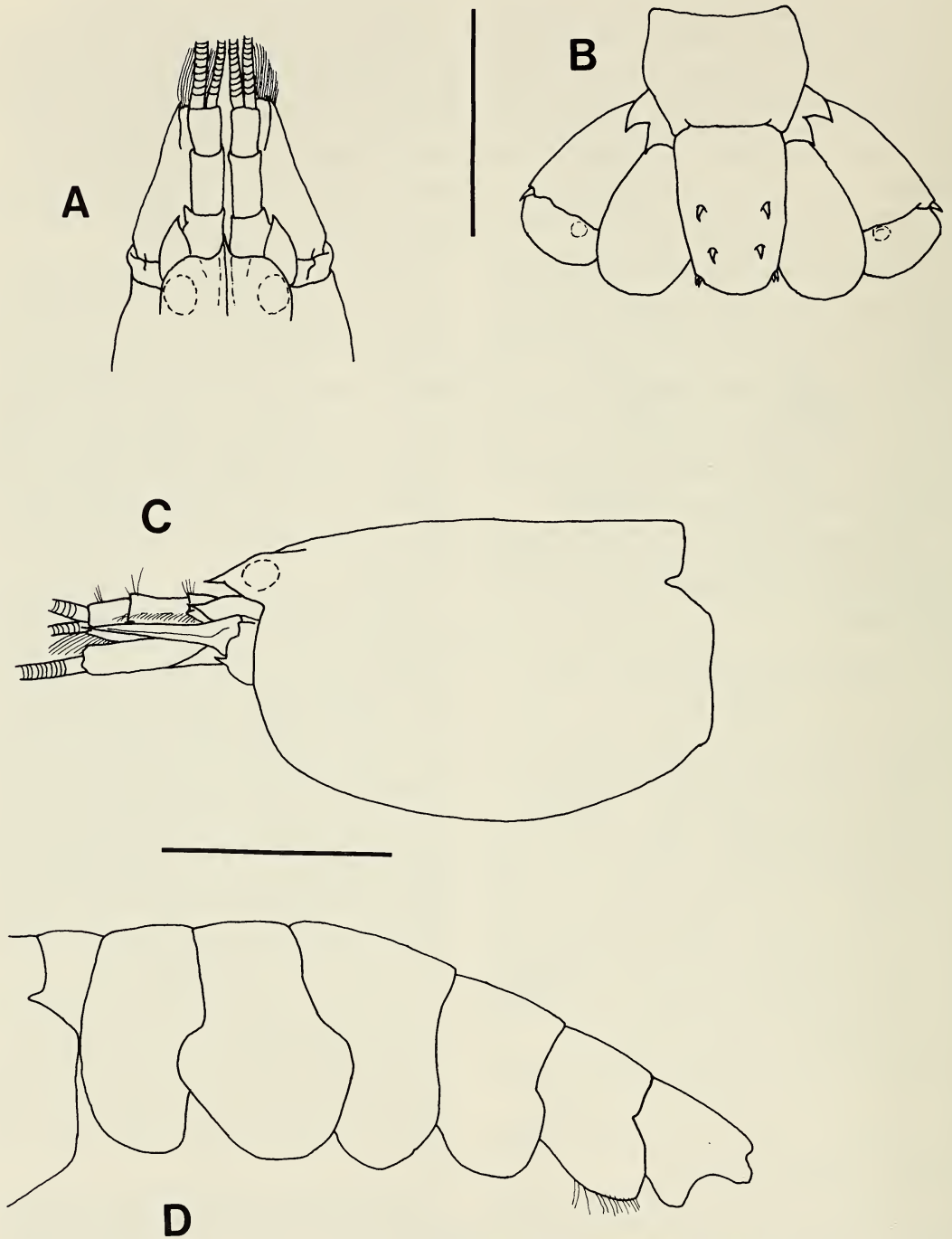


Fig. 3. *Alpheus heterochaelis* Say, 1818. A-L, Adult male (neotype) from Fort St. George Inlet, 8 miles south of Amelia Island, Florida (TL = 31 mm). A, anterior carapace and antennae, dorsal; B, sixth abdominal somite, telson and uropods, dorsal; C, carapace and antennae, lateral; D, abdominal pleura, lateral. Bar indicates 5 mm.

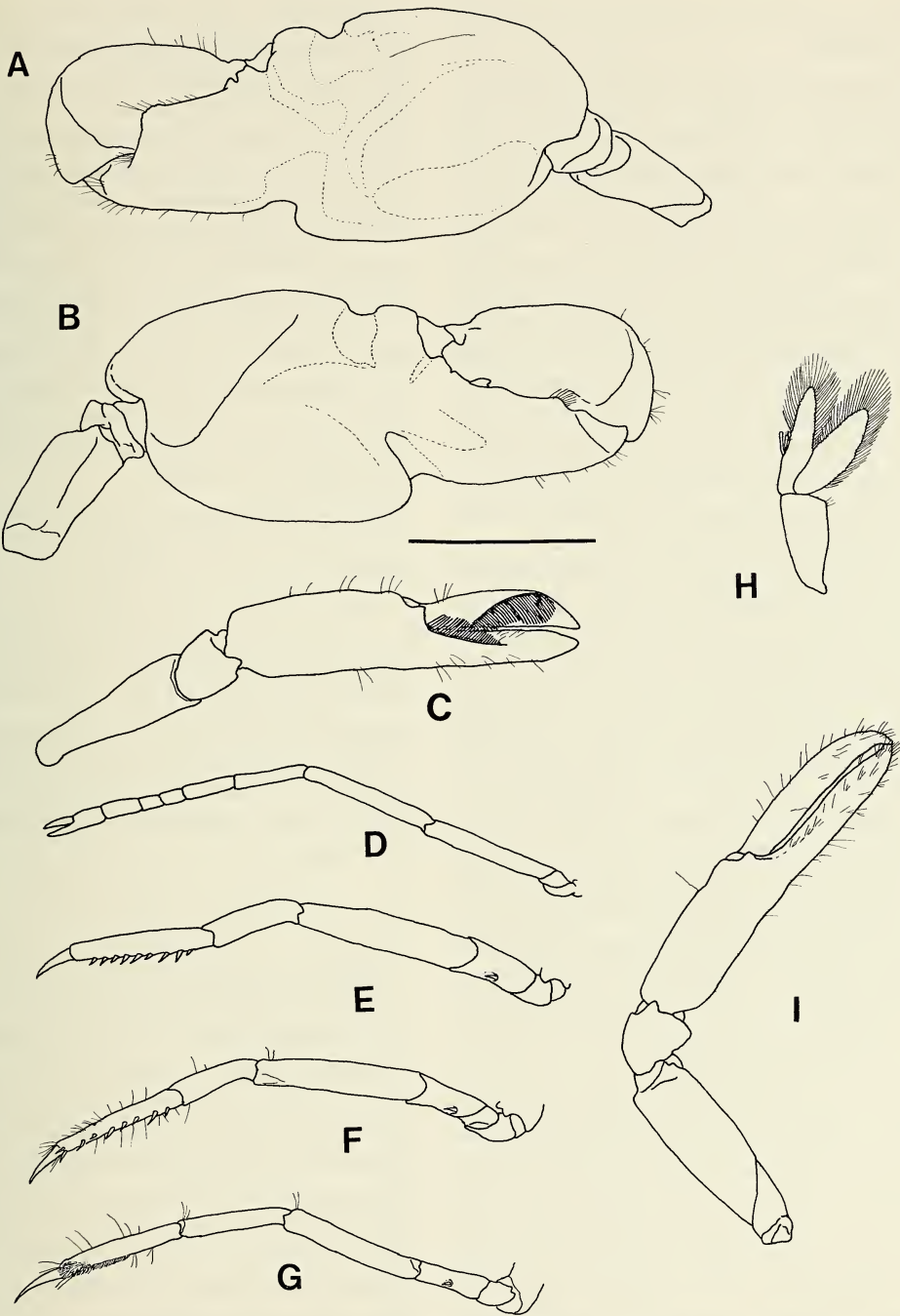


Fig. 4. *Alpheus heterochaelis*. A, major first pereopod (right), dorsal; B, same, ventral; C, minor first pereopod (left); D, left second pereopod; E, left third pereopod; F, left fourth pereopod; G, left fifth pereopod; H, left second pleopod; I, Adult female from Beaufort, NC, minor first (left) pereopod. Bar indicates 5 mm.

reaching end of antennal peduncle; terminal article setose.

First pereopods strongly chelate and unequal; merus unarmed distoventrally. Major chela (Fig. 4A, B) thick; propodus length 0.45 times total body length (range 0.29–0.61); upper and lower margins deeply notched proximal to articulation of dactyl, upper notch width about 0.07 of propodus length, lower notch width about 0.10 of propodus length; maximum propodus height about 0.45 times length; dactyl length about 0.35 times propodus length; hand height with dactyl closed about 0.32 times propodus length; dactyl with upper distal margin rounded, opposable margin with molar process tilted at angle to axis of dactyl; sculpture of propodus as figured, with upper and lower notches forming saddle-like depressions (extending 0.07 and 0.14 times length of propodus, respectively) into the lateral surfaces of propodus; upper notch positioned about 0.5 the length of propodus, lower notch positioned about 0.67; distal end of propodus rounded. Minor chela sexually dimorphic (Fig. 4C, I). Male minor chela balaeniceps-shaped, having setose crest on dactyl and accessory crest on opposable margin of the propodus; propodus 0.32 times total body length (range 0.22–0.40 for specimens examined); propodus height about 0.24 times length in males, 0.19 times length in females; dactyl length about 0.45 times that of propodus length in males, and about 0.5 in females.

Second pereopods (Fig. 4D) slender and weakly chelate; carpus subdivided into 5 articles decreasing in length as follows (numbered from the proximal end): 1, 2, 5, 3 = 4. Third to fifth pereopods (Fig. 4E, F, G) with ventral movable spine on ischium; dactyls simple; third pereopod propodus with 9 or 10 stout spines, fourth with 8 stout spines; fifth pereopod with 7 spines on propodus, with several lateral bands of comb-like setae extending on distal half. Second pleopod of male with appendix masculina shorter than appendix interna (Fig. 4H).

Coloration.—Overall olive green to brown, often with blue tones around orbits, distal half of abdomen, and telson; body speckled with tiny brown or red-brown spots. Major chela olive green with pale area at lower center of palm; raised areas of palm and opposable margin of fixed finger very dark green; upper and lower notches pale yellow to pale blue; inner surface of major chela white to pale blue; fingertips pale yellow or white. Minor chela olive green. Second to fifth pereopods translucent to pale blue, lightly speckled with reddish brown spots. Telson colored as abdomen; exopod of uropods blue on distal segment; endopod of uropods blue distally.

Size.—Neotype total length 31 mm. Total length for males ranging 16 to 45 mm, females ranging 18 to 57 mm.

Range.—Lower Chesapeake Bay southward and westward into the Gulf of Mexico; Cuba; Curaçao (Williams 1984); Bermuda (Verrill 1922); Surinam (Chace 1972); southward to Paraíba (Christoffersen 1984).

Habitat.—Intertidal and shallow waters in bays and other quiet waters consisting of mud bottoms with oyster clumps or rocks and rubble.

Discussion

Although *Alpheus angulatus* and *A. heterochaelis* are morphologically similar, they are not closely related. *Alpheus heterochaelis* and *A. angulatus* were referred to as *Alpheus* group A and group B, respectively in McClure & Greenbaum (1994), where the two species are shown to be highly divergent electrophoretically. *Alpheus heterochaelis* was the most common species that the author collected from Texas and from North Carolina. This species differs from the other Edwardsii-group *Alpheus* mentioned herein in that *A. heterochaelis* possesses a balaeniceps-type minor claw in males, and a movable spine on the ventral surface of the ischium of the fifth pereopod. *Alpheus heterochaelis* is further distinguished from *A.*

angulatus in that the rostro-orbital area in the former lacks posteriorly abrupt adrostral depressions and lacks the broad triangular area of the carapace from which the rostrum terminates posteriorly.

Material of *A. estuariensis* was examined from Port Isabel and Gilchrist, Texas, and from Mississippi Sound, Alabama, as well as the Gulf of Mexico material used by Christoffersen (1984). *Alpheus estuariensis* was not found in this survey, and thus is probably of uncommon occurrence in the northern Gulf of Mexico. *Alpheus estuariensis* is distinguishable from *A. heterochaelis* in that it lacks the balaeniceps-type minor claw in males, and lacks the movable spine on the ischium of the fifth pereopod. In addition, the minor claw of *A. estuariensis* is very slender relative to that of *A. heterochaelis*.

Alpheus angulatus was the most common species that the author collected from Florida and from Louisiana, and has apparently been mistaken for *Alpheus heterochaelis* in a number of museum collections. This is because they are both similarly colored, and commonly taken in a single sampling (both have been collected simultaneously at most of the author's collecting localities).

In one case, *Alpheus angulatus* has been mistaken for *A. estuariensis* by Christoffersen (1984). One of the specimens referred to as *A. estuariensis* (USNM 98137) from Louisiana represents *A. angulatus* and not *A. estuariensis*. *Alpheus angulatus* differs from *A. estuariensis* in that the former has a more robust minor claw, whereas the spine on the merus of the first pereopod is lacking in *A. estuariensis*. In addition, the upper and lower notches of the major chela are wider of *A. estuariensis* than those of *A. heterochaelis* and of *A. angulatus*, and the distal end of the propodus is sharply truncated in *A. estuariensis*.

Alpheus angulatus has previously been referred to as the Carolinian *A. armillatus* (Hay & Shore 1918; Knowlton 1970; Chace 1972; Williams 1965, 1984). Except by examining

the color pattern, the two species are difficult to distinguish. Both *A. armillatus* and *A. angulatus* have the typical *A. armillatus*-type rostrum, consisting of a broad, flattened triangular area posteriorly, and posteriorly abrupt adrostral furrows. Milne-Edwards' (1837) description of *A. armillatus* was brief and lacking in detail. However, the locality was given as the Antilles. The species was named "the banded *Alpheus*" for its conspicuous banded color pattern; this pattern is lacking in *A. angulatus*. Verrill (1922) stated that *A. armillatus* from Bermuda, when recently caught, was identifiable by its conspicuous transverse bands of white on the body and rings of color on the legs and antennae, and provided a photograph (plate 20, fig. 4b) showing such a pattern. Zeiller (1974, p. 76) provided a color photograph of *A. armillatus* revealing the conspicuous banded pattern on the abdomen, with the body and chelae colored overall brown speckled with white. In *A. angulatus*, the body is darker and speckled with dark red-brown spots, with speckling lacking on the chelae.

Hay & Shore (1918) listed *A. angulatus* as *A. armillatus* from North Carolina. Although the author was informed that Hay & Shore's (1918) collection may no longer exist (R. B. Manning, pers. comm.), the color description by Hay & Shore for the *A. armillatus* from Beaufort, North Carolina, matches that of *A. angulatus*. In addition, the figures provided by Hay & Shore of *A. armillatus* match *A. angulatus* with respect to the shape of the rostrum and minor chela. They also mentioned the rarity of this species at Beaufort, North Carolina, which also confirms the authors' findings (one *A. angulatus* individual was caught with 54 *A. heterochaelis* individuals). The color pattern difference between the Carolinian *A. armillatus* and the tropical *A. armillatus* also led Knowlton (1970) to speculate that the Carolinian form may represent a separate species.

The likelihood that *A. armillatus*, as cur-

rently known, represents a species complex seems more plausible now than ever, since differences in color patterns have been demonstrated to have systematic importance in *Alpheus* (Knowlton & Mills 1992). Hendrix (1971) described three color morphs of *A. armillatus* from Miami, Florida (the normal banded pattern, a blue-grey morph, and a yellow morph), and suggested that they may represent distinct species. The author was unable to locate the specimens used by Hendrix (1971), so confirmation is lacking if any of his color morphs of *A. armillatus* from the Miami region correspond with *A. angulatus*.

Hendrix (1971) mentioned in his description that *A. armillatus* (all three color morphs included) had a movable ventral spine on the ischium of the fifth pereopod, which is lacking in *A. angulatus*. Specimens of *A. armillatus* from the Smithsonian-Bredin Expedition (Chace 1972) examined from the Leeward Islands (Lesser Antilles) contain such a spine (appearing more conspicuous in smaller specimens), and also differ from *A. angulatus* in the shape of the ventral margin of the carapace; the latter having a pronounced ventral angle posterior to the second pereopods (Fig. 1C) lacking in the Antillian specimens. Other specimens identified as *A. armillatus* by Chace (1972) from the east coast of the Yucatan peninsula, Mexico, had characteristics matching *A. angulatus* (color pattern information was lacking). In addition, specimens from Haiti identified as *A. armillatus* by Coutière (MNHN-Na 2171) match the characteristics present for *A. angulatus*.

Hendrix (1971) provided a description of *A. nuttingi* (Schmitt, 1924) as the first record of that species from the continental U.S.A. His description differs from the original description of the holotype in that the latter lacks a spine on the merus of the first pereopods; this spine is present both on *A. nuttingi* and *A. angulatus*. However, *A. angulatus* differs from *A. nuttingi* (both of Schmitt 1924, and Hendrix 1971) in that *A. angulatus* possesses movable spines on the is-

chium of the third and fourth pereopods, and the "*A. armillatus*-type" rostrum is absent in *A. nuttingi*.

Alpheus normanni Kingsley, a "Macrochirus-group" species, was examined from South Padre Island, Texas, Dauphin Island, Alabama, and Crystal River, Florida. This species is mentioned here because it too has occasionally been labeled as *A. heterochaelis* in some collections. This is probably due to both *A. normanni* and *A. heterochaelis* having the balaeniceps-type minor claw in males or have both been taken simultaneously. *Alpheus normanni* is distinguished from the Edwardsii-group species mentioned herein in that the major chela of *A. normanni* lacks a lower notch, being only notched dorsally; the dorsal notch is sharply undercut proximally. In addition, *A. normanni* has angularly produced ocular hoods anteriorly, not smooth or evenly rounded as in these Edwardsii-group species (Hendrix 1971). It is also brighter green in color relative to *A. heterochaelis* and *A. angulatus*.

The geographic range of *A. heterochaelis* is apparently widespread throughout the temperate and tropical western Atlantic. Despite past taxonomic ambiguity surrounding this species, records confirm the presence of *A. heterochaelis* from eastern and southeastern North America, the Caribbean region, eastern Central America, and northeastern South America. However, *A. armillatus* should now be considered to have a tropical distribution. Previous records of *A. armillatus* from temperate North America correspond with *A. angulatus*; the latter differs from the former in color pattern and in some discrete characters. The geographic range of *A. angulatus* includes the Gulf of Mexico and northwestern Atlantic, and appears to extend into the Caribbean region. Additional ranges of *A. angulatus* are not currently known. The geographic range of *A. estuariensis* appears just as Christoffersen (1984) described, although this species does not seem to be abundant in the northern Gulf of Mexico.

Originally, a single Edwardsii-group *Al-*

pheus species, *A. heterochaelis*, was known in coastal waters from the northern Gulf of Mexico and northwestern Atlantic. Prior to this study two such species, *A. heterochaelis* and *A. estuariensis*, had been reported from the northern Gulf of Mexico. In this study, *A. angulatus* was found to be equally as common as *A. heterochaelis* and more common than *A. estuariensis* in the northern Gulf of Mexico and northwestern Atlantic. The new species resembles *A. nuttingi*, and strongly resembles *A. armillatus*, both of which may in fact consist of more than one species throughout the western Atlantic. In short, the taxonomic and biogeographic relationships existing for western Atlantic alpheids is far from being resolved.

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Appendix

Material Examined

Alpheus heterochaelis.—Collected Material: Texas: South Padre Island, Laguna Madre, north of Brazos-Santiago Pass near old Coast Guard Station, 0.5 m, $n = 31$, 17 Apr 1993; Port Aransas, north jetty at Saint Joseph Island, intertidal, $n = 19$, 18 Dec 1991; Galveston Bay, off Sportsman's Road, 0.5 m, $n = 14$, 14 Sep 1991, South jetty, 0.5 m, $n = 1$, 17 Jan 1992. Alabama: Dauphin Island, Mobile Bay, 0.5 m, $n = 4$. Florida: Pensacola, Escambia Bay, 0.5 m, $n = 1$, 18, 19 Mar, 1993; Apalachicola Bay, St. George Island State Park, 1.0–1.5 m, $n = 3$, 25 May, 1992; Panacea, $n = 5$, 26 Feb, 1992; Fort St. George Inlet, 8 miles south of Amelia Island, intertidal, $n = 1$ (neotype, USNM 268646), 25 May, 1992. North Carolina: Beaufort, near Duke Marine Lab, 0.5 m, $n = 54$, 25, 26 Jun 1993. Borrowed Material: Texas: USNM 72186, Ranson Island, $n = 1$; USNM 82116, Galveston, Offat's Bayou, $n = 2$; TAI 166, Salt Lake, Indianola, $n = 1$; TAI 167, Port Isabel, $n = 1$; TAI 169, Bahia Azul, $n = 1$; TAI 551, Bahia Azul, $n = 1$. Mississippi: USNM 64243, Dier Island, $n = 2$. Alabama: MESC 6179-3671, Mobile Bay, $n = 2$; MESC 6179-3672, Pt. Pines, $n = 2$; MESC uncat., Dauphin Island, airport marsh, $n = 2$. Florida: USNM 57635, Key West, $n = 2$; MESC 6179-5143, St. Joseph Bay, $n = 1$; FBSC I 110, Bush Key, Pinellas Co., $n = 3$; FBSC I 188, Bush Key, $n = 2$; FBSC I 364, Egmont Key, Pinellas Co., $n = 8$; FBSC I 1496 Boca Ciega Bay, $n = 1$; FBSC I 2177, Tampa Bay, $n = 1$; FBSC I 2177 Tampa Bay, $n = 1$; FBSC I 5126, Bush Key, $n = 1$; FBSC I 6244, Pumpkin Bay, Collier Co., $n = 1$; FBSC I 6338, Pakalatchee Bay, $n = 1$.

= 7; FBSC I 6378 Mullet Key, Pinellas Co., $n = 1$; FBSC I 7628, Sawyer and Sistu Keys, Boca Ciega Bay, $n = 12$; FBSC I 7685, Crystal River, $n = 2$; FBSC I 14419, W. McIlvaine Bay, $n = 1$; FBSC I 7745, Crystal River, $n = 12$. Georgia: USNM 181864, 181865, 181866, 181867, Sapelo Island, $n = 1$ each.

Alpheus angulatus, new species.—Collected Material: Texas: South Padre Island, Laguna Madre, north of Brazos-Santiago Pass near old Coast Guard Station, 0.5 m, $n = 2$, 4 Jul 1992 (holotype, USNM 266804 and paratype, USNM 266805); $n = 2$, 17 Apr, 1993; Port Aransas, north jetty at Saint Joseph Island, intertidal, $n = 3$, 18 Dec 1991; Galveston Bay, off Sportsman's Road, 0.5 m, $n = 2$, 14 Sep 1991, South jetty, 0.5 m, $n = 4$, 17 Jan, 1992. Louisiana: Terrebonne Bay, Lighthouse island south of LUMCON-Cocodrie, 0.5 m, $n = 34$, 19 Jul 1993; Florida: Pensacola, Escambia Bay, 0.5 m, $n = 45$, 18, 19 Mar 1993; Apalachicola Bay, St. George Island State Park, 1.0–1.5 m, $n = 28$, 25 May 1992; Panacea, $n = 1$, 26 Feb 1992; Fort St. George Inlet, 8 miles south of Amelia Island, intertidal, $n = 34$, 25 May 1992. North Carolina: Beaufort, near Duke Marine Lab, 0.5 m, $n = 1$, 25, 26 Jun 1993. Borrowed Material: Texas: TAI 168, Mustang Island, $n = 1$. Louisiana: USNM 98138, Lake Ponchartrain, $n = 1$. Alabama: MESC uncat., west end Dauphin Island (subsample), $n = 3$. Florida: USNM 57635, Key West, $n = 1$; FBSC I 1293 Tierra Verde, Pinellas Co., $n = 1$; FBSC I 2901, St. George Bay near Apalachicola, $n = 3$; FBSC I 2931, Magnolia Beach, Andrews Bay, $n = 2$; FBSC I 3626, Mullet Key, Pinellas Co., $n = 3$; FBSC I 6297, Gullivan Bay, Collier Co., $n = 5$; FBSC

I 7601, "Marine Research Lab", Pinellas Co., $n = 2$; FBSC I 7745 (subsample), Crystal River, $n = 1$; FBSC I, 2 miles south of Hillsborough River, $n = 1$. South Carolina: USNM 63549, Jericho Creek, $n = 7$. North Carolina: USNM 128061, Beaufort, Lennoxville Point, $n = 1$. Haiti: MNHN-Na 2171, $n = 2$. Mexico: USNM 135891, Quintana Roo, Ascension Bay, $n = 12$.

Alpheus estuariensis.—Borrowed Material: Brazil: USNM 144014, Sao Paulo, paratypes, $n = 3$; USNM 25800, Mamanquape, paratype, $n = 1$; USNM 222042, $n = 4$; MESC 6179-10461, Raiba, $n = 4$. CUBA: USNM 96455, Laguna de Paso Malo, $n = 3$. U.S.A.: Texas: USNM 63546, Jetty at Galveston Bay (Evermann 1891 coll.), $n = 2$; TAI uncat., Port Isabel, $n = 4$; LU uncat., East Galveston Bay at Gilchrist, $n = 4$. Louisiana: USNM 98137, Lake Pontchartrain, $n = 1$. Alabama: MESC uncat., Mississippi Sound, $n = 1$. Florida: USNM 90957, Duval Co., $n = 4$.

Alpheus armillatus.—Borrowed Material: Lesser Antilles: USNM 135869, Leeward Islands, Guadeloupe, $n = 14$; USNM 135870 (subsample), Leeward Islands, Antigua, $n = 4$.

Alpheus nuttingi.—Borrowed Material: USNM 68700, Holotype and 2 additional specimens from Barbados, W. Schmitt, 1918.

Alpheus normanni.—Collected Material: Texas: South Padre Island, Laguna Madre, north of Brazos-Santiago Pass near old Coast Guard Station, 0.5 m, $n = 3$, 17 Apr 1993. Borrowed Material: Alabama: MESC uncat., "Mussels 2-1", $n = 3$; MESC uncat., west end Dauphin Island (subsample), $n = 1$. Florida: FBSC I 7745 (subsample), Crystal River, $n = 1$.